OXYGEN CONSUMPTION IN ECHINODERMS FROM SEVERAL GEOGRAPHICAL LOCATIONS, WITH PARTICULAR REFERENCE TO THE ECHINOIDEA [1]

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Little information is available on respiration of echinoderms (Bliss and Skinner, 1963; Prosser and Brown, 1962). This study presents data obtained for the five classes of living echinoderms from several geographical locations, including the Monterey Peninsula, California; Punta Banda and Puertecitos, Baja California, Mexico; Savai'i, Western Samoa; St. John, U. S. Virgin Islands; and Dunedin, New Zealand. Articles by Farmanfarmaian (1966), Moore (1966), and Lewis (1967), point out the general lack of information concerning whole body respiration (oxygen consumption) in all but a few echinoids. Concurrent with an investigation of the respiratory physiology of the purple sea urchin, *Strongylocentrotus purpuratus,* in relation to reproduction, and while engaged in brief excursions to Western Samoa and to the U. S. Virgin Islands, the author was able to obtain whole body oxygen consumption data for several tropical and temperate echinoderms. In addition, laboratory studies were conducted to compare the respiratory physiology of the Pacific Coast deep water echinoid, *Allocentrotus fragilis*, and the purple sea urchin, *S. purpuratus*. This comparison provides additional information concerning the relative contributions of specific body components to whole body respiration in echinoids.

MATERIALS AND METHODS

The investigations on location were conducted with freshly collected animals according to the methods described in Webster and Giese, 1974. Closed chamber respirometry was conducted with the YSI oxygen electrode at the temperatures at which the animals were collected. All oxygen depletion experiments were of two hours' duration, and readings were taken at half-hour intervals. Large animals were tested singly in the respirometer, and small individuals were used in groups of three to six, and their weights were averaged for the calculation of the Q_{O_2}.

Laboratory investigations were conducted with the Beckman oxygen electrode apparatus described in Webster and Giese, 1974. All data presented represent a minimum of three experiments with at least three individuals of each species. Where a wide size range was investigated, the extremes are indicated. In most cases animals of similar size within a species were used, and average wet weights are indicated. Animals tested in the laboratory were held without food in aquaria for at least one week prior to experimentation.

Laboratory investigations of *Allocentrotus fragilis* were conducted according to the methods described for *S. purpuratus*. The Beckman polarographic macro-oxygen electrode was used for determinations of whole body oxygen consumption and was coupled to a potentiometric strip chart recorder to produce a continuous print-out of the oxygen depletion curve. The Instrumentation Laboratories, Inc. #17365 needle oxygen electrode was used for determinations of perivisceral fluid oxygen partial pressure ($pvfO_2$), and was coupled to the chart recorder.

Collections of *A. fragilis* were made in April, 1971, and in February, 1972, with a beam trawl from the R. V. Proteus of Stanford University. These collections were made at a depth of about 150 meters at 36° 41′ N., 122° 04′ W., off the Monterey Peninsula, California. Specimens of *A. fragilis* were held in dark aquaria at 6° C for several days prior to use in these investigations.

Data for *Evechinus chloroticus* and *Goniocidaris umbraculum* were obtained at Dunedin, New Zealand by William Johnson of the Hopkins Marine Station. Animals were held in the laboratory at 13° C for several days prior to use in the investigation.

Eupentacta quinquesemita was collected from among tubes of chaetopterid polychaetes of wharf pilings in Monterey Harbor. *Parastichopus californicus*

TABLE I

Q_{O_2} of echinoderms from several geographical locations

Class, species	Q_{O_2} ($\mu l/g/hr$)	Wet weight (g)	Temp. (C)	Location
Asteroidea				
Dermasterias imbricata	7.5	23.5	13	Monterey, California
Leptasterias aequalis	26.8	1–2	13	Monterey, California
Mediaster aequalis	15.3	15.3	13	Monterey, California
Orthasterias columbians	25.4	20.8	13	Monterey, California
Patiria miniata	10.5	11.6	13	Monterey, California
Pisaster brevispinus	12.3	19.9	13	Monterey, California
Pisaster giganteus	25.4	1.3	13	Monterey, California
Pycnopodia helianthoides	9.8	26.2	13	Monterey, California
Zoroaster evermanni	5.6	52.9	8	Monterey, California
*Astropecten aramtus**	17.4	27.1	16	Punta Banda, B. C., Mexico
*Heliaster kubiniji**	17.8	106.2	16	Puertecitos, B. C., Mexico
*Linkia laevigata**	2.2	100.3	23	Savai'i, Western Samoa
*Coscinasteria calamaria***	9.8	33–81	13	Dunedin, New Zealand
*Pentagonaster pulchellus***	3.8	12.0	13	Dunedin, New Zealand
Ophiuroidea				
Amphiodia occidentalis	3.0	0.5–1.0	13	Pacifica, California
Holothuroidea				
Eupentacta quinquesemita	17.5	5.5	13	Monterey, California
Leptosynapta inhaerens	13.9	2.4	13	Monterey, California
Parastichopus californicus	19.2	27.3	13	Monterey, California
Crinoidea				
Florometra serratissima	26.7	4.5	8	Monterey, California

* Data obtained in the field with freshly collected animals and the YSI oxygen electrode.

** Data obtained in the laboratory with the YSI electrode. Remainder of the data obtained in the laboratory with the Beckman oxygen electrode.

was collected from granite boulders under a kelp bed at Carmel, California. The *Leptosynapta inhaerens* is truly infaunal, and specimens were collected from damp sand during a low tide at Pacifica, California.

The *Amphiodia occidentalis* was collected from nearly anaerobic black sand under rocks at Pedro Point in Pacifica, California.

Florometra serratissima was collected by beam trawl at a depth of about 150 meters from the R. V. Proteus of Stanford University.

Experiments and Results

Oxygen consumption rates for the Asteroidea, Ophiuroidea, Holothuroidea, and Crinoidea are presented in Table I. The data for the Echinoidea are presented in Table II.

Discussion

The low Q_{O_2} exhibited by *Leptosynapta inhaerens* (Table I) may indicate a heavy reliance upon anaerobic respiration, particularly during low tides when water circulation under the rocks is minimal. In addition to the lower Q_{O_2}, other adaptions such as vermiformity and the loss of some internal complexity are demonstrated by the infaunal *L. inhaerens* as compared with the two epifaunal species. These relationships were found among infaunal as compared with epifaunal anemones by Sassaman and Mangum (1972). Lewis (1967) found the same to be true in tropical echinoids.

The relatively high Q_{O_2} of the crinoid, *Florometra serratissima,* may be due to its high level of activity. When disturbed, this animal exhibits active swimming behavior. Some activity persisted in the respirometer during the oxygen depletion experiments, and may be responsible for the relatively high Q_{O_2} recorded. The relatively high index of living material in this species may also be a factor, although determinations of body component indices were not made.

TABLE II

Q_{O_2} of echinoids from several geographical locations

Species	Q_{O_2} ($\mu l/g/hr$)	Wet weight (g)	Temp. (C)	Location
Echinoidea				
Allocentrotus fragilis*	5.17	50.4	8	Monterey, California
Strongylocentrorus purpuratus*	8.00	55.0	13	Pigeon Point, California
Strongylocentrorus franciscanus*	6.72	44.7	13	Pigeon Point, California
Lytechinus anamesus	14.90	3.7	16	Punta Banda, B. C., Mexico
Echinometra mathaei	4.70	28.0	23	Savai'i, Western Samoa
Echinometra lucunter	13.30	3.1	28	St. John, U. S. Virgin Is.
Tripneustes esculentus	15.60	5.2	28	St. John, U. S. Virgin Is.
Evechinus chloroticus**	5.41	760.0	13	Dunedin, New Zealand
Goniocidaris umbraculum**	4.00	12.1	13	Dunedin, New Zealand

* Data obtained with Beckman oxygen electrode in the laboratory.
** Data obtained in the laboratory with YSI oxygen electrode by William Johnson, Hopkins Marine Station. Remainder of the data obtained in the field with YSI oxygen electrode. Method described in text. (Webster and Giese, 1974.)

Reference to Table I indicates that in the asteroids, as in the echinoids, the highest oxygen consumption rates appear among the smallest individuals, regardless of the environmental temperatures, a fact well in keeping with information on all types of animals (Prosser and Brown, 1962). In fact, the lowest Q_{O_2} is found in *Linkia laevigata* at 23° C, the warmest temperature of any of the areas studies. The relatively large size of these individuals may be of greater importance than the ambient temperature in determining the Q_{O_2} of the animal. Of the species of asteroids investigated at Monterey, California (13° C), the smallest individuals exhibit the highest Q_{O_2}. It must be noted, however, that other factors which may have an effect on oxygen consumption have not been considered. These include activity, nutritional condition, and differences in microhabitat.

Among the echinoids (Table II), with the exception of *Echinometra mathaei*, the warm-water species exhibit a uniformly higher Q_{O_2} than their cold-water counterparts. All oxygen consumption rates are within the same order of magnitude found for *S. purpuratus* (Webster and Giese, 1974). It should be noted that the highest oxygen consumption rates are found among the smaller sea urchins tested, a fact which must be considered in addition to the warmer environmental temperatures of these species, in interpreting these data.

The comparatively low Q_{O_2} of *E. mathaei* is of interest as it is lower (at 28° C) than that of *S. purpuratus* (at 13° C) and *A. fragilis* (at 8° C). In light of the warmer environmental temperature and smaller size of the *E. mathaei*, it would be expected to exhibit a higher Q_{O_2} (Lewis, 1967).

The comparison of *S. purpuratus* and *A. fragilis* (Table III) reflects basic differences in the body components of these species which may account for the observed differences between them in respiratory physiology. The comparison of body wall indices shows that of *A. fragilis* to be less than half that of *S. purpuratus* (25.16 and 55.00, respectively). Because 90% or more of the whole body Q_{O_2} is attributable to the body wall component in *S. purpuratus*, little oxygen is left for transport to the perivisceral coelom and internal tissues (Webster and Giese, 1974), resulting in the low perivisceral fluid oxygen partial pressure ($PvfO_2$) of 45 mm Hg. The $PvfO_2$ of *A. fragilis* at 115 mm Hg is much higher, and can be attributed to the low body wall index which leaves substantially more oxygen for transport to the internal tissues. Body wall oxygen consumption in both species is from two to three times the whole body Q_{O_2} (Table III).

In his study of *Evechinus chloroticus*, Johnson found that the body wall Q_{O_2} was lower than that for the whole animal (3.04 $\mu l/g/hr$ for the body wall, 5.41 $\mu l/g/hr$ for the whole animal). This is contrary to the results for *S. purpuratus* and *A. fragilis*, and may have its explanation in the very large size and high gonad

TABLE III

A comparison of S. purpuratus *with* A. fragilis: *factors of significance to the respiratory physiology of echinoids*

Species	Q_{O_2} ($\mu l/g/hr$)	Body Wall Index	$PvfO_2$ mm Hg	Body Wall Q_{O_2} ($\mu l/g/hr$)	Temp. (C)
A. fragilis	5.17	25.16	115	12.7	8
S. purpuratus	8.00	55.00	45	22.0	13

TABLE IV

The gonad index and whole body Q_{O_2} for five Allocentrotus fragilis *at 8° C*

Gonad index	Whole body Q_{O_2} ($\mu l/g/hr$)
2.75	6.98
2.43	5.05
4.00	4.06
5.09	8.62
7.42	7.08

index of the *Evechinus chloroticus* tested. Additional data will be required for the resolution of this question.

Although the conclusion depends upon additional supporting data, it appears that there is no relationship between whole body oxygen consumption and reproductive condition (gonad index) in *Allocentrotus fragilis* (Table IV). These data are in agreement with those concerning whole body Q_{O_2} and the gonad index in *S. purpuratus* (Webster and Giese, 1974). Unfortunately, collections were not possible during the peak of the reproductive cycle in *A. fragilis* (November and December) because of storms, and tests were not made at this critical part of the reproductive cycle. However, between the highest (7.42) and lowest (2.43) periods of the gonad index recorded, no significant differences in perivisceral fluid ppO_2 are found. The $PvfO_2$ is 115–120 mm Hg regardless of the gonad index within the range tested. $PvfO_2$ is less variable in *A. fragilis* than in *S. purpuratus*.

Lewis (1967) found higher rates among tropical, as compared with temperate echinoids. Farmanfarmaian (1966) reports higher Q_{O_2} for *Arbacia* and *Strongylocentrotus* at 20° C than for *Echinocardium* at 15° C. Belman and Giese (1974) report a Q_{O_2} for an antarctic echinoid, *Sterechinus neumayeri*, comparable to that of temperate echinoids, and lower than that of most tropical echinoids. As stated by Kinne (1964), however, it must be recognized that an animal reacts to its total environment rather than to a single entity such as temperature, and the combined effects of two or more components of the environment must often be considered. Body size, nutritional condition, activity, and microhabitat may all be factors in determining the Q_{O_2} of any particular echinoid (Farmanfarmaian, 1966). The Q_{O_2} of epifaunal forms is higher than that of their infaunal counterparts. That this is true for anemones is demonstrated by Sassaman and Mangum (1972) and for tropical echinoids by Lewis (1967).

The prediction that tropical echinoids have a higher Q_{O_2} than temperate species holds true for all those tested except *Echinometra mathaei* from Western Samoa (Table II). Rather than reflecting higher rates under warmer environmental conditions, these data may reflect the generally smaller body size of the tropical echinoids in this study. The comparatively low Q_{O_2} exhibited by *E. mathaei* defies explanation, although the average weight of 28.0 g is much larger than the average weights of the other tropical species studied. The *E. mathaei*, with a Q_{O_2} of 4.70 $\mu l/g/hr$ at 23° C, are respiring at about half the rate of *S. purpuratus* of similar size at 13° C.

TABLE V

Oxygen consumption of representative aquatic species from several phyla

Phylum, species	Qo_2 ($\mu l/g/hr$)	Temp. (C)	Reference
Porifera			
Microciona prolifera	115	37	Bliss and Skinner, 1963
Cnidaria			
Astrangia danae	26		Sassaman and Mangum, 1972
Haloclava producta	30		Sassaman and Mangum, 1972
Metridium senile	100		Sassaman and Mangum, 1972
Annelida			
Arctonoe vittata	27–167	13	Webster, unpublished
Diopatra cuprea	50		Mangum, Kushins and Sassaman, 1970
Mollusca			
Cryptochiton stelleri	6	13	Webster, unpublished
Helix pomatia	45–3070	28	Kerkut and Laverack, 1956
Arthropoda (Crustacea)			
Cambarus clarkii	200	25	Maloeuf, 1937
Cirolana harfordi	95–463	13	Webster, unpublished
Gnathophausia ingens	48	4.5	Childress, 1971
Spirontocaris securifrons	77	6.5	Fox, 1936
Opisthopus transversus	11–153	13	Webster, unpublished
Echinodermata			
Antedon petasus	24	8	Fox, 1936
Arbacia punctulata	16	20	Boolootian and Cantor, 1965
Asterias forbesii	100	25	Maloeuf, 1937
Holothuria forskali	2.7	10	Fox, 1936
Ophiura terturata	11	10	Fox, 1936
Ophiura terturata	21	17	Fox, 1936
Pteraster tesselatus	10.5	10–12	Johansen and Peterson, 1971
Chordata (Vertebrata)			
Ambystoma maculatum	120	20	Whitford and Hutchinson, 1967

In comparing the oxygen consumption data for all of the tropical species, it is evident that they have oxygen consumption rates that are similar to those of temperate (*S. purpuratus* and *S. franciscanus*) and Antarctic (*Sterechinus neumayeri*) echinoids of equivalent size, suggesting their adaptation to higher temperature. Certainly this reflects some form of thermal adaptation (see Hochachka and Somero, 1973) among tropical, temperate, and polar echinoderms, but the biochemical basis of this has yet to be determined.

In his table of comparative oxygen consumption rates among representatives of several major phyla, Nicol (1967) cites data in which the echinoderms exhibit similarly low rates in comparison to the other groups. I believe the relatively low Qo_2 exhibited by the echinoderms as a group is based on three factors. This, of course, assumes that other factors which might affect oxygen consumption (nutrition, activity, reproductive condition, *etc.*) are equal, an assumption which is questionable at best.

The first factor is the relatively inefficient transport of oxygen to the internal tissues of echinoderms. This inefficiency is probably most pronounced among the echinoids, and least important among the holothuroids with respiratory trees

and respiratory pigments. Among the phyla listed in Table V, either a circulatory system including respiratory pigments supplies the internal tissues, or ambient sea water may be circulated as in the Anthozoa, past both sides of a relatively thin body wall; or, in the case of the sponges, ambient water is circulated in close proximity to all living cells. Thus, it appears that among these groups (Table V) the echinoderms exhibit the lowest level of efficiency in providing the internal tissues and body fluids with oxygen.

A second factor is the relatively high proportion of metabolically inert skeletal material in some echinoderms (the ophiuroids, in particular) and the large volume of perivisceral fluid, with its very low metabolic activity, in others (echinoids and holothuroids). Thus, as has been shown for the echinoids (Webster and Giese, 1975), only a small component of the body (the body wall tissue) accounts for 90% of the oxygen consumption of the animal.

A third possible factor resulting in the relatively low Q_{O_2} among echinoderms is their low level of activity when compared with many other phyla. It is difficult to differentiate standard from active metabolic rates among the echinoids. The authors cited in Table V, however, often point out the differences in standard and active metabolism, resulting in the highly variable Q_{O_2} data given for some species.

SUMMARY

1. Whole body oxygen consumption data are determined for a variety of echinoid, asteroid and holothuroid species, and for one ophiuroid and one crinoid.

2. Comparisons of tropical and temperate asteroids indicate no correlation of oxygen consumption rate with environmental temperature among the individuals tested. As is the case for echinoids, body size appears to be an important factor in determining the Q_{O_2} of a particular species.

3. Whole body oxygen consumption data are determined for several temperate and tropical echinoid species, and for a deep-water echinoid of the Pacific Coast.

4. A comparison of respiratory physiology in *S. purpuratus* and *A. fragilis* is made, with particular attention to the body wall and gonad indices.

5. Comparisons of tropical and temperate echinoid oxygen consumption rates reveal that, when animals of similar size are compared, the Q_{O_2} of the tropical forms is similar to that of their temperate counterparts.

6. The generally smaller body size of the tropical species tested results in the higher oxygen consumption rates which they exhibit as compared with temperate echinoids.

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